

Bonn. zool. Beitr.	Bd. 50	H. 1–2	S. 89–101	Bonn, Dezember 2001
--------------------	--------	--------	-----------	---------------------

## **Enchytraeidae as prey of Dolichopodidae, recent and in Baltic amber (Oligochaeta; Diptera)**

Hans Ulrich & Rüdiger M. Schmelz

**Abstract.** A piece of Baltic amber with two inclusions, an enchytraeid worm fragment and a dolichopodid fly, is described. The morphological account of the enchytraeid fragment includes details on number, shape and distribution of the chaetae. It is the first detailed description of an oligochaete in Baltic amber. Field observations of recent Dolichopodidae preying on Enchytraeidae are reported. The available evidence suggests that the fossil worm fragment was carried into the resin by the fly as its prey. Thus, this piece provides a fossil record of predation by Dolichopodidae on Enchytraeidae, and points to a plausible explanation as to how the oligochaete worms found as rare inclusions in Baltic amber could have been trapped in the resin.

**Key words.** Baltic amber, Enchytraeidae, Dolichopodidae, predation.

### **Introduction**

The present paper reports on a piece of Baltic amber with two inclusions, a dolichopodid fly and an enchytraeid worm, and on recent observations by which the common fate of the two animals may be explained.

Recent Dolichopodidae were observed as adults preying on Enchytraeidae. As will be shown in the relevant paragraphs, the piece of amber presents several traits which may be taken for evidence that the worm was carried into the resin by the fly as its prey.

The authors of this joint paper are specialists in the families involved, the Enchytraeidae (R.M.S.) and Dolichopodidae (H.U.), respectively. Each studied the representatives of his group among the available material, both recent and fossil, and will discuss his observations. Thus, each is responsible for the section concerned with the worm and the fly, respectively.

A preliminary report of our observations was presented at the 4th International Congress of Dipterology in Oxford, U.K., September 1998 (Ulrich & Schmelz 1998). Two of our photos taken from the amber piece were published in colour, with a concise explanatory text based on our interpretation, in the amber book by Weitschat & Wichard, 1998, pp. 54–55. [N.B. The author of the dolichopodid species is not Meigen but Meunier.]

### **The amber piece**

The specimen (Fig. 1) was offered to the senior author and purchased by him for an amber collection of Diptera to be built up and deposited at his home institution (ZFMK). According to information from the dealer, it originated from the Eastern Baltic deposits in Kaliningrad District.

The amber piece was flattened and polished to facilitate the study of both objects, the worm and the fly. The embedding of the inclusions is rather good. Within the piece, a curved plane roughly parallel to its upper surface marks the joint or cleft between two layers formed by successive resin flows. In the figures it is seen from its convex side, and is discernible by a delimited area around the worm (Fig. 4), reflexions, and by a stellate hair fibre (the contorted fibre left of the worm) and some smaller particles lying in it. The worm is lying flat in this plane, whereas the fly is lying on its left side and slightly oblique, with its legs partly in and its trunk and wings above the convex surface. Apparently this was the surface of the resin on which the animals were trapped. Although sticky, however, the resin must have been rather viscous, for neither of the two animals sank in: the worm remained lying flat on its surface, while most of the fly remained outside before both were completely embedded by a sub-sequent flow.

The left side of the fly's trunk, i.e. the reverse when viewed as in Fig. 1, is covered by white emulsion. Apparently this was the off-light side of the inclusion facing the substrate covered by the resin (Schlüter & Kühne 1975), just as the concave side of the curved plane mentioned above faced the substrate. So, both structures point to the same direction and confirm that Fig. 1 is a view on the outer surface of the resin mass as it was when the animals were trapped.

The position of both inclusions on the same plane proves that both were trapped at the same time or, at least, in the short time between two resin flows.



Fig. 1. The dolichopodid fly, *Gheynia bifurcata* ♀, and the enchytraeid worm (right) lying in the amber piece.

### Authentic or forged?

A forgery can be excluded for various reasons:

- The piece contains stellate hairs and individual fibres thereof, which proves that it consists of amber and not of any artificial mounting medium.
- It is rather clear, without any disturbances around the inclusions which could be explained as traces of an artificial implantation.
- The fly is covered on its lower side by a white emulsion produced by exudation from its body, as frequently found on amber inclusions.
- It belongs to a genus, *Gheynia* Meunier, which is unknown from the World's recent fauna but rather common in Baltic amber.
- Since predation on worms by Dolichopodidae is not widely known, it is hard to imagine that a forger could have known about it and made an artificial mount of predator and prey. The dealer was not aware either of the biological context when he offered the specimen, and although it was explained to him, he still offered it at a moderate price which would have been too cheap for a perfect forgery.
- Last but not least, the following paragraphs will show that all evidence fits together to allow a reconstruction of what happened in the last hours of the animals' lives so well, that it can hardly be a product of forgery.

### The fly (H. Ulrich)

#### Recent observations in the field

Dolichopodidae with Enchytraeidae as prey were observed repeatedly since 1968 in woods in southern and western Germany (Murnauer Moos, Upper Bavaria; Härtsfeld, Swabian Jura; Eifel). Some of the flies were photographed, some were taken together with their prey and preserved in ethanol. The observations include the following species and sexes (classification after Ulrich 1981): Rhaphiinae: *Rhaphium crassipes* (Meigen) ♀, *Argyra auricollis* (Meigen) ♀, and *Argyra* sp. indet. ♀; Dolichopodinae: *Dolichopus atripes* Meigen ♀, *D. nigricornis* Meigen sensu Parent [= *discifer* Stannius] ♀ and ♂, *D. popularis* Wiedemann ♀ and ♂, *D. ungulatus* (Linnaeus) ♀, *Gymnopternus aerosus* (Fallén) ♀, *Hypophyllus crinipes* (Staeger) ♀, and *H. obscurellus* (Fallén) ♀.

Most of the flies were seen perching on leaves of low herbage with a worm held by the proboscis (Figs 2–3), but some were observed on the soil searching for prey and catching worms. Preying on Enchytraeidae appears to be a common habit of adult Dolichopodidae, which can be observed wherever the flies are abundant and the worms are accessible to them.

The normal procedure is as follows: A fly roves about on the soil in search of prey, walking with some quick and short steps and stopping, walking again, sometimes leaping a few centimetres or flying to another place. It inspects small hollows and cracks in the soil, finds at last an accessible worm in its tube, stoops down and apparently seizes the worm with its proboscis.

The Dolichopodidae are known to use their labella for grasping prey and for holding it firmly while sucking it out. This was first described and figured for *Medetera* Fischer and a psychodid fly as prey, by Fischer (1819) who, however, misunderstood his observations as swallowing. This error was corrected by Macquart



Fig. 2. *Dolichopus unguulatus* ♀ with an enchytraeid. The worm has been grasped at some distance from its end which is folded back. Swabian Jura, Härtsfeld, 10 July 1970.

(1828a: 15–16, 1828b: 227–228). The mouthparts of Dolichopodidae have been studied repeatedly. A classical account of their structure and function was published by Snodgrass (1922), extensive comparative descriptions by Cregan (1941) and Satô (1991).

Having seized the worm, the fly tries to pull it out from its tube. This, if successful, is normally done in two steps: first the worm is pulled forth for part of its length, subsequently a second attempt is made to pull it out as a whole. If the fly succeeds and the worm is exposed for all its length, a heavy struggle follows: the worm squirms vigorously, beats around and has a good chance to be released by the fly and not to be attacked again. The larger the worm is in proportion to the fly, the better is its chance to get free. During the fly's second attempt it may happen that the worm is torn in two pieces and the fly gets a fragment only to feed on.

If the fly keeps hold of the worm, it will normally take off and fly to a leaf to feed on its prey there. The worm is hanging down from the fly's proboscis, held by the labella. It squirms as long as it can, while it is rhythmically moved up and down by the fly, apparently by alternate retraction and protraction of the labium. By these movements the end of the prey held between the labella is probably pushed against the epipharyngeal armature which serves to lacerate its body wall (see Snodgrass 1922).

In all cases observed by me, the flies did not use their legs to support the labella in seizing or holding the prey. However, a female of *Argyra auricollis* did use a fore leg





Fig. 3. *Argyra auricollis* ♀ with an enchytraeid. The fly is warding off the squirming worm with its left fore leg. Note the soil particles adhering to the worm. Upper Bavaria, Murnauer Moos, 23 July 1968.

to keep a squirming worm off its head (Fig. 3). Similar observations by Cregan (1941: 14) on *Dolichopus ramifer* Loew may be interpreted so. In other cases (*Hypophyllus obscurellus*) it seemed that the fly tried to press the worm against the soil with its legs during the struggle after capture.

In contrast, *Hydrophorus* Fallén has been observed holding insect prey with the fore legs (Aldrich 1911: 45, Williams 1939: 307, Peterson 1960: 270), which are used both for predation and, by the male in a pair, for holding the female (Dyte 1988; Lunau, unpublished photo; inferred from sexual dimorphism by Aldrich 1911: 48). Use of the fore legs as predatory legs has also been reported for other hydrophorine genera, viz., *Scellus* Loew, *Hydatostega* Philippi, *Thinophilus* Wahlberg, and *Aphrosylus* Haliday (Doane 1907, Harmston 1948, Roubaud 1903).

Most of the flies met with a worm were females. This conforms to the common experience that female flies are more voracious as predators than males, and can be explained by the need of protein food for production of eggs. However, males did feed on Enchytraeidae too, as observed in *Dolichopus nigricornis* and *D. popularis*.

While searching for Enchytraeidae, some of the flies met insects which would have been a suitable prey too, but apparently did not take notice of them. It appears that the worms were more attractive. Nevertheless, the published record of Dolichopodidae preying on oligochaete worms is scanty, whereas preying on insects has been recorded frequently. Wahlberg (1845, quoted in English by Lundbeck 1912: 15) described predation on Naididae by Dolichopodidae of various subfamilies on a muddy

seashore. Aldrich (1922) mentions oligochaete worms besides dipterous larvae as prey of the adults, Cregan (1941) observed *Dolichopus* Latreille extracting annelids from the soil, Lunau (1993) mentions Enchytraeidae and Tubificidae among the prey of *Poecilobothrus* Mik. Observations by Negrobov and Pogonin on oligochaete worms, apparently Enchytraeidae, as predominant food of Dolichopodidae are reported and demonstrated by photos in an unpublished thesis (Pogonin 1984). (I wish to thank A. Stark who called my attention to this account, and O.P. Negrobov who sent me copies of the relevant paragraph.)

### The fossil fly

The fly is a female and was identified *Gheynia bifurcata* Meunier. It is 2 mm long.

*Gheynia* can be recognized by the shape of the third antennal joint (postpedicel, Stuckenberg 1999), with projections above and below the insertion of the arista (stylus) which are longer in the male, short but still discernible in the female (see figures in Meunier 1908a: 8 and 1908b: 57). A similar shape is found in some recent species of *Chrysotus* Meigen, particularly so in *C. furcatus* Robinson and *C. hilburni* Woodley (see Robinson 1964 and Woodley 1996). Meunier (1907–1908) regarded *Gheynia* (wrongly emended to *Gheynius*) as an aberrant representative of his genus *Palaechrysotus* [now recognized as a junior synonym of *Paleomedeterus* Meunier]. He placed both close to *Chrysotus* and included them in a common key to species (1907: 199, 209–210; 1908a: 8–9; 1908b: 9, 13–15, 56–59). However, the specimen of *Gheynia* discussed here, as well as other specimens examined from Baltic amber, have an anterior pre-apical bristle on each mid and hind femur as in Sympycninae, whereas the recent *Chrysotus* species cited above agree, according to their descriptions, with the ground pattern of *Chrysotus* and the Diaphorinae in lacking this bristle and having instead an anteroventral row of bristles before the end of the hind femur. So, *Gheynia* cannot be a close relative of *Chrysotus* and even less of *C. furcatus* and *C. hilburni*, and the peculiar antennal shape must have evolved independently. It may be closer to the recent sympycnine *Scotiomyia* Meuffels & Grootaert, whose antennae resemble those of the female (see Meuffels & Grootaert 1997). Selivanova & Negrobov (1997) placed *Gheynia* in the Peloropeodinae.

As stated in the description of the amber piece, the fly is lying on its left side above the surface on which it was trapped, and its left (lower) side is completely covered with white emulsion. In addition, there are small globular masses of emulsion on the right (upper) side above both thoracic spiracles and a thin layer on the right pleural membrane and around the tip of the abdomen. Evidently the thoracic and abdominal spiracles and the anus were the openings through which fluids oozed from the body.

The fly is lying at some distance from the worm with its legs pointing to the worm. The right hind leg is broken between the metatarsus and the second tarsomere, and the distal fragment is separated from the proximal part by a distance equalling the length of the tibia.

All these observations can be explained by the following scenario: The fly with its prey, alighting on the resin, touched the surface with its legs, got stuck and dropped the prey which fell onto the sticky surface. The fly then tilted over to its left side and, pushed by the legs, drifted away from its original position. The right hind leg may have broken when the fly tried to pull it out from the resin. When a tarsus is torn in a living fly or a recently killed one, the unguitractor tendon may adhere to the distal

fragment and be drawn out from the proximal part to connect both. Apparently this did not happen in the fossil fly, since no trace of tendon could be discerned in this position. It is likely that the tendon would have been preserved in the amber and should be visible if it was lying exposed.

### The worm

(R. M. Schmelz)

#### Material from recent observations

Recent enchytraeid worms preserved in ethanol were identified as far as possible. They had been collected by the senior author at one of the localities of his field observations, in Upper Bavaria, Murnauer Moos, in wood with *Impatiens noli-tangere* as the dominating element of the herbal layer, 1 and 8 July 1968. The identifications are given below.

A sample collected from the upper stratum of the soil near the surface where Dolichopodidae were searching for prey contained species of *Henlea* Michaelsen, 1889 (23 specimens), *Fridericia* Michaelsen, 1889 (3 specimens) and *Buchholzia* Michaelsen, 1887 (1 specimen). Six worms preserved together with their predators (*Dolichopus popularis* 1♂ 3♀, *Hypophyllus crinipes* ♀, *Argyra auricollis* ♀) were all *Henlea* sp., including 1 complete adult worm with 40 segments and two fragments with hind end.

It is uncertain though unlikely that dolichopodids specifically select *Henlea* species as prey. The selection goes possibly rather by size and occasion. Many *Henlea* species live especially close to the soil surface, up to the Of-horizon. Furthermore, the presence of *Impatiens noli-tangere* indicates a habitat where *Henlea* sp. can be found in high numbers (Schmelz, pers. obs.). In the collection of enchytraeids from the Murnauer Moos, *Henlea* sp. is the dominant genus, but the sample is not representative as the worms were eye-picked and not sampled quantitatively.

#### The fossil worm

The object is observable from both sides of the amber piece, but the chaetal arrangement is clearly visible only from one side, as viewed in Fig. 4, whereas refractions blur the microscopical details on the other side.

The worm is not complete; one end forms a wound (lower end in Fig. 4, left in Fig. 5). The wound is not closed, shreds of tissue project outside. It is surrounded by a small and highly refractile field, consisting of a mixture of tissue and body fluid. This field is surrounded by a much larger quasi-circular field lying in the same curved plane as the worm fragment and the fly, which was apparently formed by coelomic fluid that had oozed from the wound and spread on the surface of the resin. Its texture is grainy with some scattered granular concentrations, possibly coelomocytes. About half of the worm fragment lies within this field, the wounded end in its centre (Fig. 4, lower half), whereas the other half is outside with its free end rounded and uninjured. As no prostomium and no internal differentiation of the terminal seven segments are discernible, the intact end is most likely the rear end and the fragment the posterior part of the worm.





Fig. 4. The worm fragment lying in the field of putative coelomic fluid. Same view as in Fig. 1, higher magnification in darkfield illumination. Intact hind end of worm above, injured end below.

The worm fragment is c.  $1400\ \mu\text{m}$  long and  $100\text{--}200\ \mu\text{m}$  wide. It consists of 31 chaetigerous segments, considerably contracted towards the injured end. There are four chaetal bundles per segment, two lateral and two ventral ones. The dorsal half of the body surface is without chaetae. When viewed from the side with the best optical resolution (Fig. 5), the dorsal body surface is visible in the posterior half of the fragment. Only one lateral chaetal bundle per segment is visible here. Due to a successive torsion of the object, three chaetal bundles are discernible on the opposite side of the fragment, two ventral and one lateral.

There are three chaetae per bundle in all observable cases, in fan-shaped arrangement. The distal part of each chaeta is strongly curved, with a simple, pointed tip (Fig. 5, bottom right). The proximal part inside the body is not observable. The chaetae are fairly stout, estimated lengths and diameters are  $40\text{--}50\ \mu\text{m}$  and approx.  $3\ \mu\text{m}$  respectively. The lateral and ventral chaetae are alike. The chaetae appear to be thicker in lateral view than in top view.

Each segment has a strong secondary annulation. There are 5–8 annuli per segment. The annuli on chaetal level are most prominent. Intersegmental furrows are observable in some segments as clearly marked furrows exactly halfway between the chaetae.

The internal organization of the worm is indistinguishable. Dark brownish food pellets are visible inside the body over the entire length of the fragment including the posterior end.



### Systematic position

A posterior end of an oligochaete worm that shows not much more than the chaetal pattern cannot be identified with certainty, because usually mature specimens with complete anterior ends are needed to identify the species. This applies to recent specimens and all the more to a c. 40 million year old fragment. However, if a similar recent worm fragment from a terrestrial subtropical habitat was found it would be determined as an enchytraeid. All observable characters except the strong intersegmental annulation – possibly an artefact due to desiccation before complete inclusion – agree with what is only found in Enchytraeidae. Earthworms (e.g. Lumbricidae, Megascolecidae) are excluded by the presence of three chaetae per bundle and by the size of the fragment which is very small for an earthworm, even if it was a hatchling. Other 'microdrile' oligochaete taxa, most of them aquatic, are excluded by the following combination of characters which is found only in Enchytraeidae: presence of lateral (instead of dorsal) chaetal bundles, lateral and ventral chaetae alike, three per bundle, chaetae curved with simple-pointed tips. Furthermore, the peculiar distribution pattern of the chaetae indicates that the worm belongs to a truly-soil-dwelling rather than an aquatic species: the lateral (rather than dorsal) position of the uppermost chaetal bundles is not found in aquatic microdrile oligochaetes and can be explained as an adaptation to locomotion in terrestrial habitats (Schmelz, in prep.).

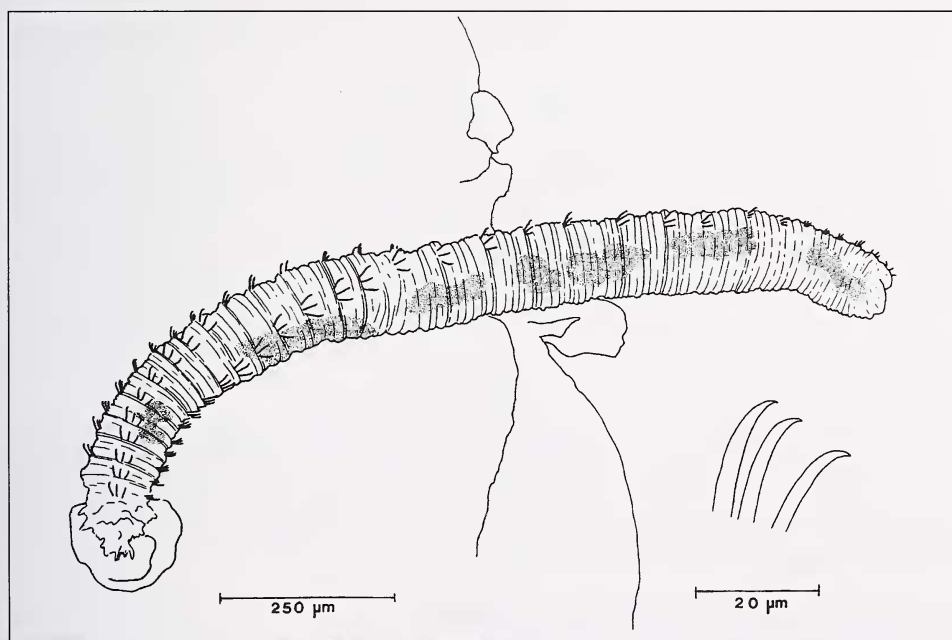


Fig. 5. Details of the worm fragment. Same view as in Fig. 4, but turned so that the intact hind end points to the right. The irregular vertical lines above and below the mid-region of the fragment mark the refractile periphery of the field of coelomic fluid. Bottom right: Distal parts of the chaetae of one bundle, lateral view.

Among all known recent genera of Enchytraeidae, the specimen fits best in *Buchholzia*, the only genus with the character combination of lateral (rather than dorsal) chaetal bundles, more than two chaetae per bundle and curved chaetal tips, but the specimen may also belong to an extinct or a yet unknown recent genus. It should also be stressed that the key criterion that decides on the identity of an enchytraeid, the location of the reproductive organs, is unknown here; so the possibility remains that the specimen belongs to a different family, unknown and extinct, of terrestrial oligochaetes.

Since Menge's description of *Enchytraeus sepultus* from Baltic amber (1866), small and undifferentiated vermiform inclusions have repeatedly been identified as oligochaetes and more specifically as enchytraeids (Bachofen-Echt 1949, Larsson 1978), although this was mainly inferred from recent observations in habitats comparable to the Baltic amber forest. Wunderlich (1996: 205) points at the easy confusion of these "enchytraeids" with nematodes or dipteran larvae. Rarely were characters observed in the inclusions that would prove the oligochaete nature of the object. Chaetae are mentioned only once, but not described (Menge 1866). A clitellum is seen in Bachofen-Echt (1949, fig. 17. p. 22). The present amber inclusion of an oligochaete fragment is the first one from which not only the existence of chaetae is recorded but also their number, shape and distribution is described.

#### What happened to the worm?

To ask how the worm could be embedded as a fragment, means to ask if it was wounded after being trapped in the resin, or before. Generally, an animal embedded in a fragmentary state might have been partly exposed before it was completely surrounded by resin, and its exposed parts eaten by a predator. This is unlikely in the present case since the worm, lying flat in the surface, did not offer a point of attack to predators, or otherwise the surface of the resin would have been stirred up which would have left traces. So we must assume that the worm was wounded before it got in contact with the resin. This, however, would be unlikely if the worm was either surprised by resin flowing over it or actively crept into the resin, as discussed by Larsson (1978: 117). And, if so, it would lie deep in the amber near the lower surface of the flow. The dolichopodid fly lying beside the fragment offers the explanation that the worm was torn by the fly when it was pulled out from the soil. Shortly after, both must have been trapped on the resin, otherwise there would not have been much coelomic fluid left to spread on the surface.

It may be remarkable that the fragment is the posterior part of the worm. This conforms to the observation that the two available fragments of recent Enchytraeidae preserved together with their predators are posterior parts, too. If the few cases allow the conclusion that the fly normally gets the posterior end, this is another support for our assumption that the worm was the fly's prey.

#### The worm and the fly – concluding remarks

If our experience from recent field observations is applied to the present amber inclusions and all detailed evidence to be drawn from the amber piece is taken into consideration, everything fits together to suggest that the worm was in fact carried into the resin by the fly as its prey, after it had been torn when pulled out from the

soil. As stated in the description of the amber piece, both must have been trapped at the same time or nearly so, and both came from the upper surface of the resin, i.e. the convex face.

How could an enchytraeid worm otherwise get into the resin from above? This can hardly have been by active locomotion. Unless it fell down onto the resin or was washed there by heavy rain, which is hard to imagine for an earth-living worm, it can only have been carried by another animal. The evidence points to the fly, a predator whose recent relatives prey on enchytraeids and carry them from one place to another. Female flies appear to be more active predators than males. The fossil fly is a female, and its size and mouthparts fit to the size of the prey.

If we accept this explanation, the present piece of amber with its inclusions provides evidence that Dolichopodidae preyed on Enchytraeidae already in the Upper Eocene. This was to be expected since oligochaete worms were present in the amber forest as proven by rare inclusions, and the mouthparts of Dolichopodidae in amber look like those of the recent species and were obviously appropriate for grasping prey.

For palaeohelminthology, this piece offers a plausible explanation how Enchytraeidae could get into amber, not by a rare chance but by a common biological process.

### Acknowledgements

We wish to thank C.E. Dyte for revision of our English text and critical remarks. Final stages of field work (Summer 1998) in Upper Bavaria were conducted in a nature reserve under permit A98-000014 granted to H. U. by the Landratsamt Garmisch-Partenkirchen. We are grateful to our colleague E.-G. Burmeister (Zoologische Staatssammlung München) and the regional and local authorities for their kind cooperation.

### Zusammenfassung

Ein Stück Baltischen Bernsteins, das ein Fragment einer Enchytraeide und eine Dolichopodide enthält, wird beschrieben. Zum ersten Mal wird eine detaillierte Beschreibung eines Oligochaeten aus Baltischem Bernstein geliefert, die Angaben über Anzahl, Form und Verteilung der Borsten enthält. Freilandbeobachtungen an rezenten Dolichopodiden als Prädatoren von Enchytraeiden werden geschildert. Alle verfügbaren Indizien am Bernstein sprechen dafür, daß das Wurmfragment als Beute der Fliege in das flüssige Harz geraten ist. Demnach bietet dieses Stück einen Fossilbeleg für die räuberische Ernährung der Dolichopodiden von Enchytraeiden und zeigt, auf welchem Wege Oligochaeten, die als seltene Inklusionen im Baltischen Bernstein zu finden sind, in das Harz gelangen konnten.

### References

- Aldrich, J. M. (1911): A revision of the North American species of the dipterous genus *Hydrophorus*. – *Psyche* 18: 45–70, 72–73, Pl. 8.
- Aldrich, J. M. (1922): A new genus of two-winged fly with mandible-like labella. – *Proc. ent. Soc. Wash.* 24: 145–148.
- Bachofen-Echt, A. (1949): Der Bernstein und seine Einschlüsse. – 8 + 204 pp. – Springer, Wien. – Reprint 1996, with additions by J. Wunderlich: 11 + 230 pp., Wunderlich, Straubenhardt.
- Cregan, M. B. (1941): Generic relationships of the Dolichopodidae (Diptera) based on a study of the mouth parts. – *Illinois biol. Monogr.* 18, No. 1: 68 pp.
- Doane, R. W. (1907): Notes on the habits of *Scellus virago* Ald. – *Ent. News* 18: 136–138.
- Dyte, C. E. (1988): Mate guarding and sex ratio in *Hydrophorus oceanus* (Macquart) (Diptera: Dolichopodidae). – *Entomologist* 107: 122–126.
- Evenhuis, N. L. (1997): *Litteratura taxonomica dipterorum (1758–1930)*, 2 volumes: Vol. I (A-K): ix + pp. 1–426; Vol. II (L-Z): iv + pp. 427–871. – Backhuys, Leiden.

- Fischer [-de-Waldheim], G. (1819): Notice sur une mouche carnivore, nommée Medetère. – In: Programme d'invitation à la séance publique de la Société Impériale des Naturalistes, qui aura lieu le 15 décembre, 5–11, 1 pl.
- Harmston, F. C. (1948): Dipterous predators of the mosquito in Utah and Wyoming. – Great Basin Nat. 9: 21–23.
- Larsson, S. G. (1978): Baltic amber – a palaeobiological study. – Entomograph Vol. 1: 192 pp., 12 pls. – Scandinavian Science Press, Klampenborg.
- Lunau, K. (1993): Mating behaviour in the long-legged fly *Poecilobothrus nobilitatus* L. (Diptera, Dolichopodidae): courtship behaviour, male signalling and mating success. – Zool. Beitr., (n. F.), 34 (1991/92): 465–479.
- Lundbeck, W. (1912): Diptera Danica. Genera and species of flies hitherto found in Denmark. Part IV. Dolichopodidae. – 4 + 416 pp. – Gad, Copenhagen, & Wesley, London.
- Macquart, J. (1828 a): Insectes Diptères du nord de la France. Platypézines, Dolichopodes, Empides, Hybotides. – 159 pp., 4 pls. – Danel, Lille, "1827". – (Pp. 1–76, 158 partim and pl. 1 form the separate edition of Macquart 1828 b. Dated after Evenhuis 1997.)
- Macquart, J. (1828 b): Insectes Diptères du nord de la France. Platypézines, Dolichopodes, Empides, Hybotides. – Rec. Trav. Soc. Sci. Agr. Arts Lille 1826/1827 (1827): 213–291, 1 pl. – (The Empides and Hybotides are not included. Dated after Evenhuis 1997.)
- Menge, A. (1866): Über ein Rhipidopteron und einige andere im Bernstein eingeschlossene Tiere. – Schr. naturf. Ges. Danzig, (n. F.), 1 (3–4): 2–8.
- Meuffels, H. J. G., & P. Grootaert (1997): Dolichopodidae (Diptera) from Papua New Guinea XVI. *Scotiomyia* gen. nov. a new Sympycninae genus from the rain forest with notes on the Papuan Sympycninae. – Studia dipt. 4: 247–255.
- Meunier, F. (1907–1908 a): Monographie des Dolichopodidae de l'ambre de la Baltique. – Naturaliste (Paris) 29 (1907): 197–199, 209–211, 221–222, 233–235, 245–246, 260–262, 269–271, 281–282; 30 (1908): 7–9, 21–23, 29–30, 45–46, 57–59. – (Incomplete paper, the equivalents of pp. 74–86 of the separate edition missing.)
- Meunier, F. (1908 b): Monographie des Dolichopodidae de l'ambre de la Baltique. – iii + 100 pp. – Publications du journal Le Naturaliste, Paris. – (Separate edition of Meunier 1907–1908a, with different pagination, with corrections and additions.)
- Peterson, B.V. (1960): Notes on some natural enemies of Utah black flies (Diptera: Simuliidae). – Canad. Ent. 92: 266–274.
- Pogonin, S.V. (1984): [Fauna and ecology of species of the family Dolichopodidae (Diptera) of "Stolby" natural reserve.] [In Russian.] – 73 pp. – Thesis, Voronezh State University. (Not seen in original.)
- Robinson, H. (1964): A synopsis of the Dolichopodidae (Diptera) of the Southeastern United States and adjacent regions. – Misc. Publ. ent. Soc. Amer. 4: 103–192.
- Roubaud, [E.] (1903): Sur des larves marines de Dolichopodes attribuées au genre *Aphrosylus* (Wlkr.). – Bull. Mus. Hist. nat. (Paris) 9: 338–340.
- Satô, M. (1991): Comparative morphology of the mouthparts of the family Dolichopodidae (Diptera). – Insecta matsum., (n. Ser.) 45: 49–75.
- Schlüter, T., & W. G. Kühne (1975): Die einseitige Trübung von Harzinklusen – ein Indiz gleicher Bildungsumstände. – Ent. germ. 1: 308–315.
- Selivanova, O.V., & O.P. Negrobov (1997): [The Dolichopodidae (Diptera) fauna of Baltic amber.] [In Russian.] – In: Alunov, A. F., & E. P. Nartshuk (eds): [Insecta (Diptera) in ecosystems], Papers from the 6th All-Russian Symposium of Dipterology dedicated to A. A. Stackelberg, 115–116. – Russian Academy of Sciences, Zoological Institute, St. Petersburg.
- Snodgrass, R. E. (1922): Mandible substitutes in the Dolichopodidae. – Proc. ent. Soc. Wash. 24: 148–152.
- Stuckenberg, B.R. (1999): Antennal evolution in the Brachycera (Diptera), with a reassessment of terminology relating to the flagellum. – Studia dipt. 6: 33–48.
- Ulrich, H. (1981): Zur systematischen Gliederung der Dolichopodiden (Diptera). – Bonn. zool. Beitr. 31 (1980): 385–402.
- Ulrich, H., & R. M. Schmelz (1998): Enchytraeidae (Oligochaeta) as prey of Dolichopodidae, recent and in Baltic amber. – Abstr. 4th int. Congr. Dipt. (Oxford, 1998): 231.



- Wahlberg, P. F. (1845): Några jakttagelser vid Dolichopodernes lefnadssätt, samt närmare utredning af *Rhaphium flavipalpe* Zett. – Naturhist. Tidsskr., (Ser. 2), 1: 41–46.
- Weitschat, W., & W. Wichard (1998): Atlas der Pflanzen und Tiere im Baltischen Bernstein. – 256 pp. – Pfeil, München.
- Williams, F. X. (1939): Biological studies in Hawaiian water-loving insects, Part III: Diptera or flies, B: Asteiidae, Syrphidae and Dolichopodidae. – Proc. hawaii. ent. Soc. 10: 281–315.
- Woodley, N. E. (1996): A review of the genus *Chrysotus* (Diptera: Dolichopodidae) from Bermuda. – Proc. ent. Soc. Wash. 98: 199–207.
- Wunderlich, J. (1996): Anhang. – In: Bachofen-Echt, A.: Der Bernstein und seine Einschlüsse, Reprint, 205–230. – Wunderlich, Straubenhardt.

Dr. Hans Ulrich, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, D-53113 Bonn. – Rüdiger M. Schmelz, Universität Osnabrück, FB 5, Spezielle Zoologie, D-49069 Osnabrück.